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Isolation and Interaction of ON and OFF Pathways in Human Vision: Pattern–Polarity Effects on Contrast Discrimination

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To activate selectively cortical ON and OFF pathways, I measured pattern contrast discrimination functions and manipulated contrast polarity (positive and negative) of base contrast (C) and added contrast (ΔC). C was a large, long-duration cosine mask and ΔC was a brief, localized, spatially narrow-band "D6" pattern. For same polarity C and ΔC, contrast discrimination followed a "dipper" pattern: threshold facilitation at low C and a power relation (exponent < 1.0) at high C. The facilitation is predicted from the low-contrast response of cortical neurons and seems to represent isolation of an ON or OFF pathway. Opposite polarity C and ΔC give a monotonic function. ΔC increases at low base C and remaining higher than the same-polarity function at higher C values. This represents interaction between ON and OFF pathways. Pathway isolation also occurs: a positive test is detected as a contrast increment if masked by negative contrast and a negative test is detected as a contrast decrement if masked by positive contrast. Quantitative aspects of the data suggest a subtractive interaction at low C values and a divisive interaction between pathways at high C values. Test contrast thresholds upon uniform fields of varying luminance show that both the dipper effect and most of the rise in ΔC with C are mediated in pattern-selective pathways rather than at a site of luminance adaptation. The pattern–polarity effects on contrast discrimination rule out the "channel uncertainty" explanation for the facilitation dipper. My results suggest that parallel ON and OFF pathways evolved because stimulus-produced decreases in the response of a single pathway are potentially confounded with the effects of contrast adaptation. Thus transient decreases in response in either pathway are not processed and both decreases and increases in contrast are expressed as response increases in separate pathways.

Contrast discrimination Contrast normalization ON and OFF pathways Pattern masking

INTRODUCTION

The early visual system is divided into two populations of neurons responsive either to positive or negative directions of luminance change, the ON and OFF pathways of neurophysiology (Kuffler, 1953; Schiller, 1992). These pathways are thought to mediate the perception of brightening and darkening (Jung, 1973; Fiorentini, Baumgartner, Magnussen, Schiller & Thomas, 1990). Recent perceptual experiments in which the retinal ON mechanism in monkey is blocked with 2-amino-4-phosphonobutyrate (APB) suggest that the detection of luminance increments and decrements is accomplished independently in ON and OFF pathways (Dolan & Schiller, 1994).

In this paper I present psychophysical experiments designed to isolate the ON and OFF pathways in humans. The experiments also demonstrate interaction between ON and OFF pathways. *Isolation* of a pathway means that a psychophysical threshold is based on the response of a single pathway, either ON or OFF. *Interaction* means that the response of a pathway governing threshold is also influenced by responses in the pathway of opposite polarity. I will show how pathway isolation and interaction are inferred from specific patterns of psychophysical results.

It has been difficult to infer isolation of ON and OFF pathways. For example, the issue of whether increments and decrements in luminance level are detected exclusively in ON or OFF pathways is complicated by the fact that the retinal on-center and off-center mechanisms are responsive to both luminance polarities as increases or decreases in a baseline firing rate (DeValois, Jacobs & Jones, 1962; Bowen, Pokorny, Smith & Fowler, 1992). Thus, both pathways might contribute to detection of any luminance change. This problem may be avoided if the stimuli to be detected are increments or decrements in *pattern contrast* (Tyler, Chan & Liu, 1992; Bowen & Wilson, 1994). Pattern-selective simple cortical cells have nearly zero baseline rates of firing and act as half-wave rectifiers that register either increasing or decreasing

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pattern contrast strictly as increases in firing rate (Albrecht & Hamilton, 1982; Albrecht & Geisler, 1991). In principle, an appropriately structured pattern would selectively activate the ON or OFF pathway at a cortical level.

It can also be difficult to infer interaction of pathways. Since ON and OFF pathways share a common receptoral substrate, stimulation with either lights increments or decrements would be expected to alter the sensitivity of both ON and OFF pathways (Bowen & Wilson, 1994). In my experiments, which involve the visual masking of one pattern by another one, there are cases where activation of one pathway reduces sensitivity more for opposite-polarity than for same-polarity patterns. This effect is not expected on the basis of a common receptoral input to ON and OFF pathways (Bowen & Wilson, 1994). The present experiments will characterize interaction between cortical ON and OFF pathways.

The experimental approach was developed by Bowen and Wilson (1994). We used a visual masking paradigm in which a small briefly-presented *test pattern* is detected in the presence of a large, long-duration, high-contrast cosine *mask pattern*.

As the test we used a localized patch of pattern with a horizontal luminance profile defined by the sixth derivative of a Gaussian (called a D6 pattern). This stimulus should stimulate orientation and spatial-frequency selective pathways such as the simple cells of area V1 in primate cortex (Hubel & Wiesel, 1968; Movshon, Thompson & Tolhurst, 1978). For this purpose, a D6 pattern has many desirable characteristics. It is spatially narrow-band with a one-octave bandwidth at half-height. The D6 is also localized, and thus less affected by retinal inhomogeneity than a pattern such as an extended cosine. A localized, spatially narrow-band pattern should be detected through a single tuned pathway (e.g. a homogeneous ensemble of cortical units). As such, the D6 test stimulus reduces the effects of probability summation across pathways (Phillips & Wilson, 1984) while also reducing channel uncertainty (Nachmias & Kocher, 1970). We manipulated the contrast polarity of the D6, positive or negative contrast, to tap selectively the cortical ON and OFF pathways. Horizontal luminance profiles for negative and positive D6 patterns are shown in Fig. 1.

A masking paradigm measures the extent to which a masking stimulus changes the detection threshold for a test stimulus. A change in test threshold implies that the mask affects the pathway mediating detection of the test. Wilson and I used extended cosine patterns as masks. Measured masking effects were dependent on the spatial frequency and orientation of the mask pattern. This implies that masking involves pathways at a cortical level. To favor ON vs OFF pathway activation by the mask, the test patten was centered on either a light bar or dark bar of the cosine. If test and mask had simultaneous onset, a light bar of the mask elevated contrast threshold for a negative test pattern more than it elevated threshold for a positive pattern. Conversely, threshold was more elevated for a positive than a negative test pattern with a dark bar as a mask. We interpreted these effects as an interaction between cortical ON and OFF pathways. A mask of a given contrast polarity stimulates one pathway and inhibits the pathway of opposite polarity (i.e. the pathway governing the detection threshold).

By varying the stimulus onset asynchrony (SOA) between brief test and long-duration mask [a Crawford (1947) paradigm], we also measured the time–course of the pattern–polarity interaction. The interaction is transient, occurring at simultaneous onset of test and mask. Test thresholds then decline rapidly (an effect of adaptation or gain control), and by 200 msec after mask onset, the polarity interaction is not present.

In the present work, I change the experimental focus. I will fix the SOA at zero, and investigate whether pattern–polarity interactions observed at high mask contrast occur over a wide range of mask contrast levels. I will conduct classic *contrast discrimination* experiments. A contrast discrimination experiment measures the just-detectable change in contrast (ΔC) as a function of a base contrast (C) in a simple visual pattern. The resulting contrast discrimination function has a characteristic nonmonotonic form. At very low base contrasts (about 1%), there is a remarkable decrease in ΔC below its unmasked value, a facilitation of the discrimination threshold (Campbell & Kulikowski, 1966; Nachmias & Sansbury, 1974). After reaching a minimum value, the value of ΔC rises as a power function of the base contrast C.

In this study, a D6 test pattern is the threshold contrast increment (ΔC) and a cosine mask pattern presents the base contrast (C). Manipulating the contrast polarity of the test ΔC and the mask C will rectify a significant methodological bias in the literature. Many previous studies tested essentially similar conditions: base contrast and added contrast were identical cosine patterns, equal in size and spatial frequency and presented at zero spatial phase (the added contrast was incremental) for the same interval (typically 100–500 msec) (e.g. Nachmias & Sansbury, 1974; Legge & Foley, 1980; Bradley & Ohzawa, 1986). The combination of simultaneous onset, complete temporal overlap, and contrast increments favors the ON pathway. Here I will define the characteristics of mechanisms responding to contrast decrements. In addition, my procedure involves detection of a transient, spatially-localized change in contrast within a larger and longer mask rather than an overall and simultaneous change in the contrast of a base pattern. It is thus similar to contrast discrimination in naturalistic settings where changes in pattern contrast are more likely to occur locally than globally.

I will also determine whether pattern contrast discrimination is affected by light adaptation due to local luminance variation in the base pattern as well as by its contrast. Bowen and Wilson (1994) proposed a model of pattern masking in which the threshold for a test pattern is affected at two stages: by a retinal light adaptation process (masking by luminance level) and by a subsequent cortical stage of orientation and spatial-frequency

selective filtering (masking by pattern). These stages can be separated empirically by comparing the masking effects of cosine gratings with the effects of uniform fields of the same luminance as the peak and trough of the cosine mask. In the present paper I apply this model to contrast discrimination functions. I will show that the low-contrast facilitation of ΔC is not attributable to retinal light adaptation but to pattern-selective mechanisms. I will also show that most of the increase in ΔC at higher levels of C is pattern-specific, and that same-polarity contrast discrimination isolates either the ON or the OFF pathway.

Finally, I will analyze detection for opposite polarity C and ΔC. The data will show that contrast discrimination follows a monotonic function of base contrast and not a dipper. ΔC is greater for opposite than for same polarity ΔC and C across the whole range of C. I will examine alternative interpretations of this monotonic contrast discrimination to confirm pathway isolation and interaction.

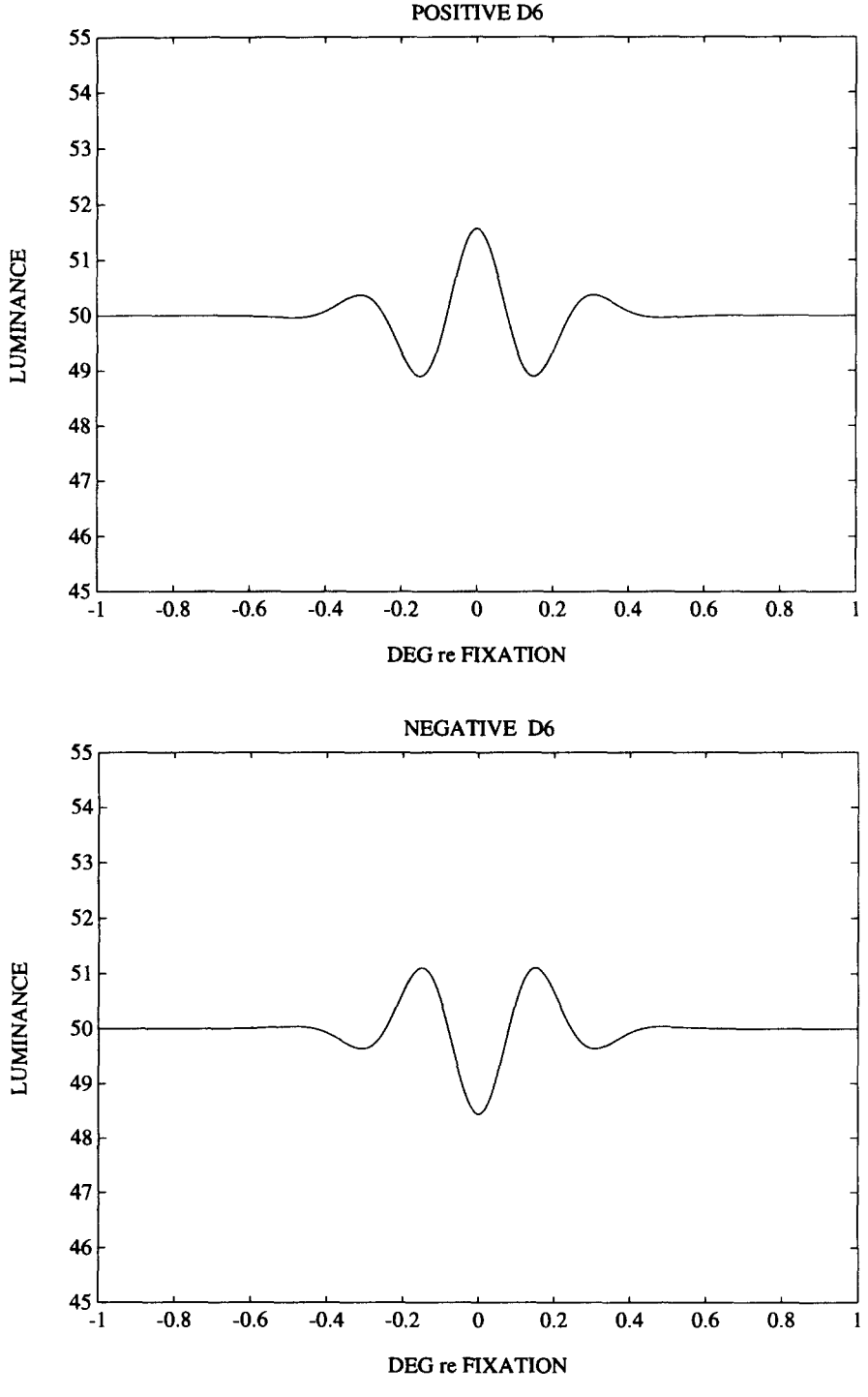

FIGURE 1. Horizontal luminance profiles of positive and negative D6 patterns such as those used in the experiments. The spatial frequency was 3 c/deg. These patterns were masked by cosine patterns of the same spatial frequency and a given D6 was centered on either a light bar or dark bar of the cosine. See text for details. The patterns shown are at 0.03 contrast; note luminance scale (units are in cd/m^2).

METHODS

Observers

The author and two graduate students in psychology were observers. The students were compensated, they were experienced with the psychophysical task, but were unaware of the purpose of the experiments. All observers wore their customary refractive correction.

Stimulus conditions to test pattern contrast discrimination

The base contrast stimulus, the *mask*, was a 5.1 deg square cosine pattern with a spatial frequency of 3 c/deg. The added contrast stimulus, the *test*, was a localized patch of pattern with a luminance profile defined by a *D*6 pattern) in the horizontal dimension multiplied by a Gaussian in the vertical dimension, as given by:

$$\mathrm{D6} = \frac{c}{15}\left\{15 - 90\left(\frac{x}{\sigma}\right)^2 + 60\left(\frac{x}{\sigma}\right)^4 - 8\left(\frac{x}{\sigma}\right)^6\right\}\exp\left[\frac{-x^2}{\sigma_x^2}\right]\exp\left[\frac{-y^2}{\sigma_y^2}\right] \quad (1)$$

where σ is a space constant for a Gaussian component (of x or y) and c is the contrast.

$$c = (L_{\mathrm{extreme}} - L_{\mathrm{mean}})/L_{\mathrm{mean}} \quad (2)$$

where L_{mean} is the mean luminance.

A D6 pattern can be either positive (incremental peak luminance) or negative (decremental peak) as indicated in Fig. 1. For a positive D6, L_{extreme} is the maximum luminance in the pattern, and c varies from 0 to 1. For a negative D6, L_{extreme} is the minimum luminance, and c varies from 0 to -1. The horizontal space constant (σ_x) determines the peak spatial frequency of the D6 [peak spatial frequency = $1.73/(\pi \cdot \sigma_x)$]. Here the peak spatial frequency was 3 c/deg, the same as the mask pattern. The vertical space constant was 44 min arc. The D6 stimulus (ΔC, the added contrast) was 30 msec in duration.

The contrast of the cosine mask was defined as for the D6 test, which is identical to the Michelson contrast for such a pattern. The cosine mask (C, the base contrast) was either 420 or 500 msec in duration, depending upon the experiment. The SOA between test onset and mask onset could be varied in 16 msec steps.

In the main experiment (Expt 1), for a range of C values, I tested four combinations of two spatial phases of C (0 deg, masking by light bar; 180 deg, masking by dark bar) and two polarities of ΔC (positive and negative D6 patterns). Thus two same-polarity and two opposite-polarity conditions tested for contrast discrimination.

In a second experiment C was a long-duration cosine pattern and ΔC was a short-duration cosine pattern. The ΔC cosine pattern was either at 0 or 180 deg spatial phase relative to the cosine mask.

Stimulus generation and viewing conditions

The presentation and sequencing of stimuli and structure of experimental trials was under computer control using software developed by Hugh Wilson and modified as needed in my laboratory. An Apple Macintosh computer controlling two 8-bit gray-scale Apple video monitors was used to present mask (C) and test (ΔC) stimuli. The monitors have a spatial resolution of 480 pixels vertically × 640 pixels horizontally. Monitors were calibrated at 151 gray levels from 0 to 160 cd/m^2 (mean luminance of 80 cd/m^2) and the resulting linear fit gave a correlation coefficient of > 0.999. A pixel dithering algorithm allowed a range of 604 gray levels to be used to generate patterns, and dithering was applied to all test patterns of 0.08 contrast or less. Each monitor screen was 7.33 deg high × 9.77 deg wide at a viewing distance of 1.25 m, and each pixel subtended 55 sec arc.

The test (ΔC) and mask (C) stimuli were presented independently on separate monitors, and the stimuli were optically combined using a prism beam splitter. The screen of each monitor was held at mean luminance (80 cd/m^2) throughout each experiment. The optically-superimposed images of the test stimulus and masking stimulus monitors gave a mean luminance at the eye of 50 cd/m^2, with the maximum contrast possible in either test or mask limited to 0.5.

During experimental runs, observers fixated the center of a 5 deg square area of the superimposed monitor screens defined by the inner tips of a vertical and a horizontal pair of black lines (0.15 deg in length). The observer viewed the superimposed screens monocularly in darkness with their head on a chin rest.

Psychophysical method

A two-interval forced-choice procedure was used to determine threshold values of ΔC. The observer initiated a trial by depressing a key on the computer keyboard. Two successive presentations of the base contrast mask occurred (separated by 1000 msec), with the 30 msec D6 pattern presented at a fixed SOA in either the first or second mask interval. The onset of each mask presentation was marked by a tone. The observer indicated which interval contained the test pattern by depressing a key. Contrast levels of ΔC were varied randomly. In a given run, five D6 contrast levels were used, selected on the basis of pilot observations. Twenty trials per level used during a given daily experimental run. The threshold for a run was determined by fitting a Quick (1974) function to the data using a maximum likelihood estimation technique. Daily thresholds were 75% correct points estimated from these functions. Final threshold values were the mean of 3–4 daily threshold values.

EXPERIMENT 1

The first experiment had two aims: (1) to measure contrast discrimination for same-polarity and opposite-polarity patterns. The stimuli consisted of either a negative or positive D6 test pattern centered upon either

a light bar or dark bar of a cosine mask. (2) To measure contrast thresholds for positive and negative D6 test patterns on uniform fields set at luminance levels corresponding to the luminance at the peak (or trough) of light (or dark) bars of a cosine mask. Contrast thresholds on uniform fields were to estimate the extent to which test threshold was elevated by luminance adaptation (Bowen & Wilson, 1994).

For aim (1), contrast thresholds (ΔC) for detecting 3 c/deg positive and negative D6 patterns were determined for a 3 c/deg cosine mask at eight contrast levels (C from 0.005 to 0.4). The mask was in 0 deg spatial phase: tests were centered on a *light bar* of the mask. The masking pattern was 420 msec, the test pattern was 30 msec, and the SOA was 0 msec (simultaneous onset of ΔC and C). Observers RWB and KC participated. I also tested masking by a *dark bar* of the cosine (180 deg spatial phase) at three cosine contrast levels (0.0125–0.2) masking) using only observer KC. Finally, I also determined both observers' contrast detection threshold for the 30 msec D6 test presented against an the unmodulated mean luminance field (a "blank mask").

For aim (2), I measured thresholds for detecting positive and negative D6 test patterns on masks consisting of homogeneous uniform fields (5.1 deg square, like the cosine patterns). Observers RWB and KC were tested with *incremental uniform fields* at several luminance levels from 50.625 to 70 cd/m^2, corresponding to the luminance level at the peak of *cosine gratings* of contrasts of 0.0125 to 0.4. Observer KC was also tested on comparable *decremental* uniform fields at luminance levels corresponding to those at the trough of cosine mask gratings for the several contrasts used in the dark bar masking condition.

Results

Cosine masking data. Figure 2 shows contrast discrimination functions for the two observers for positive D6 test stimuli (○) and negative test stimuli (●) for a 0 deg cosine mask (light bar masking). The thresholds for positive and negative D6 tests alone on the mean luminance field are plotted on the y-axis above the label "B" (for "Blank"). Both observers show nearly equal detection thresholds for positive and negative D6 patterns, as in Bowen and Wilson (1994).

When positive D6 tests increment the contrast of a light bar of the mask (○), the data follow the expected dipper function. The value of ΔC initially decreases with increasing C to a minimum, and then increases with C, eventually following a power function, with a linear relation on these double-log coordinates.

For negative D6 tests, which locally decrement the mask contrast, ΔC rises monotonically with C and then also follows a power function at high values of C. The lines superimposed on the data at high mask contrasts are regression lines for a power function fit. The exponents of the best-fitting power functions for positive and negative tests were similar for both subjects, as indicated in Table 1. The values of these exponents are also close to those that have been reported in the literature for

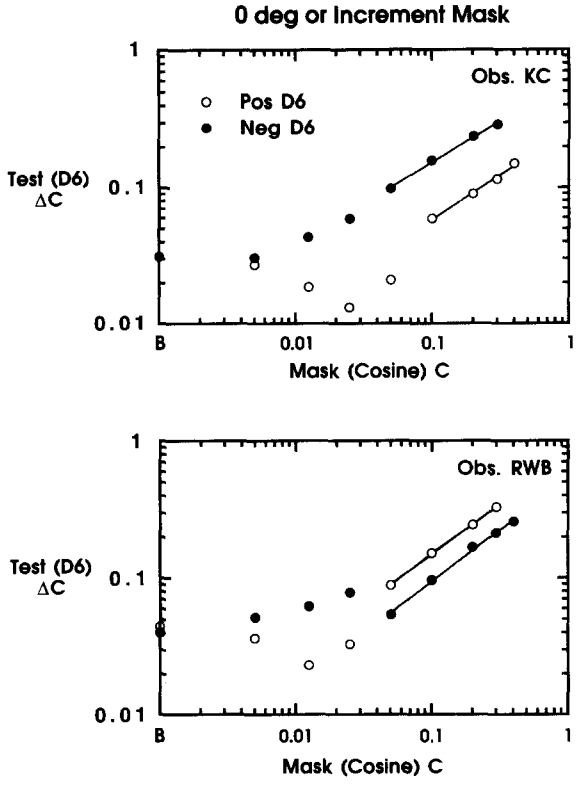

FIGURE 2. Contrast discrimination functions from Expt 1 for two observers. The functions give threshold contrast ΔC for a D6 test (positive, ○; negative, ●) as a function of the contrast C in a cosine mask. The mask was at 0 deg spatial phase; tests were centered on a light bar of the cosine. The data points plotted on the vertical axis were unmasked contrast thresholds for the tests (B, Blank). The straight lines through the high-contrast data are best-fitting power functions. See text and Table 1.

increments in the contrast of cosine patterns. Bowen and Wilson (1994) observed that at SOA = 0 msec, D6 thresholds on 0.25 contrast cosines were greater for opposite than for same-polarity test and mask. Figure 2 shows that this interaction holds over a wide range of mask contrasts.

In Fig. 2, at high base contrasts, thresholds for positive vs negative D6 tests differ by roughly 0.2 log unit for observer RWB and 0.4 log unit for observer KC. SEs for the mean data shown were nearly always <0.05 log unit (always <0.075 log unit). Statistical theory dictates that decisions about whether two data points differ should be based on the SE of the *difference* between the two means, i.e. a value that is $\sqrt{2}$ greater than the SE of either data point; and two data points will be significantly different (0.05 level) if the distance between them is 1.96 (z units) $\times \sqrt{2} \times$ the SE of a data point, or 2.77 SEs of a data point. In the present results, the criterion separation for two data points each with a SE of 0.05 log unit is roughly 0.14 log unit. There is therefore a statistically significant difference between the functions in Fig. 2 both

TABLE 1. Exponents (double-log slopes) for best-fit power functions of data in Fig. 2

	Positive ΔC	Negative ΔC
Observer KC	0.676	0.607
Observer RWB	0.753	0.729

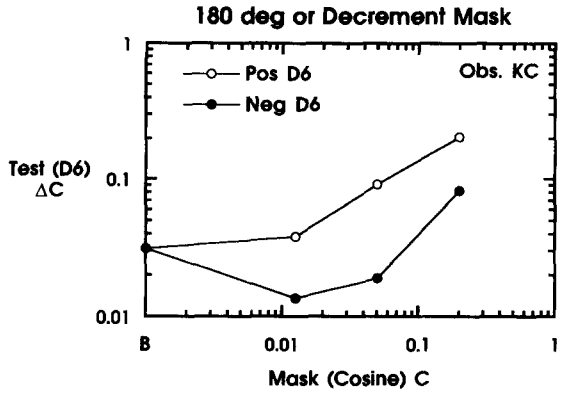

FIGURE 3. Data as in Fig. 2 except that the cosine mask was in 180 deg spatial phase so tests were centered on a dark bar of the cosine.

at high contrast and at the contrast minimum of the dipper.

Figure 3 gives data for masking by a dark bar of the cosine. These results follow the same pattern as those in Fig. 2, except that the effects of test contrast polarity are reversed: a dipper effect for negative ΔC, a monotonic effect for positive. In the Discussion, we will analyze how the data of Figs 2 and 3 and could occur for various detection schemes involving cortical ON and OFF pathways.

Georgeson and Georgeson (1987) measured a monotonic contrast discrimination function with a test consisting of contrast reversal in a cosine pattern over one cycle of a 40 Hz sine wave. The usual dipper effect was obtained with positive-contrast test and mask (both 25 msec in duration, cosine patterns, simultaneous presentation). The discrimination functions for the contrast-reversal test and normal contrast discrimination converged at high contrasts.

The Georgesons' results superficially resemble the present data for same vs opposite-polarity test and mask (Figs 2 and 3), although my functions are separated at all contrast levels. The Georgesons suggest that with a contrast-reversal test, the facilitation effects from the positive phase of the stimulus are canceled by the effects of the negative phase. Therefore, it seems likely that a similar monotonic function would be obtained if the test were reversed in time to become a contrast decrement followed by a contrast increment. Further, it seems unlikely that test contrast reversal upon positive base contrast would isolate either the ON or the OFF pathway. In the Discussion, I will argue that the present masking conditions do achieve pathway isolation.

Uniform field masking data. Bowen and Wilson (1994) proposed that the masking effect of a stimulus such as a cosine grating could be factored into two components: masking by luminance level (e.g. the luminance level prevailing at the peak of a test pattern) and masking by the stimulus pattern itself. We proposed that masking by light level is an early (retinal) luminance-adaptation process and that masking by pattern was a later (cortical) pattern-selective process. The overall threshold elevation due to a cosine mask results from a serial (multiplicative) concatenation of early and late processes.

In the analysis, masking effects are defined as *threshold shift*. This is the threshold for a test on a mask divided by the unmasked threshold for the test (e.g. on a steady mean-luminance field). A threshold shift of 1.0 indicates no masking effect. A threshold shift of > 1.0 indicates that a mask raises test threshold by that factor, and a shift of < 1.0 indicates facilitation by a mask, a lowering of test threshold.

The putative early and late processes determine the total masking effect of a cosine pattern. The threshold shift due to uniform fields of the same luminance as the peak and trough of the cosine grating estimates the effect of the early process responding to point-by-point variation of luminance in the cosine mask. The threshold shift due to the late pattern-selective process is estimated by dividing cosine mask threshold shift by the shift due to a uniform field of the peak or trough luminance:

$$\text{Threshold shift}_{(\text{cortical})} = \text{Threshold shift}_{(\text{cosine})}/\text{Threshold shift}_{(\text{uniform field})}. \quad (3)$$

Empirically, this ratio expresses the factor by the overall masking effect of a pattern exceeds the masking effect due to a uniform luminance level at peak or trough of the pattern.

The use of uniform fields to estimate the masking effect due to retinal luminance adaptation is controversial, judging from the comments of one referee for this paper. I justify the uniform field stimulus from experiments indicating that light adaptation occurs on an extremely fine spatial scale, comparable to the size of individual cone receptors (MacLeod *et al.*, 1992). The masking effects of essentially local light adaptation on a D6 test with peak positioned on a peak or trough of a cosine mask should be well represented by the effects of a uniform field at peak or trough luminance.

On the other hand, the referee suggested a scenario in which the adaptation effect may be local in spatial scale, but the overall patterning or spatial distribution of retinal luminance adaptation could produce a significant masking effect prior to a pattern-selective processing stage. The idea is, first, that adaptation locally reduces sensitivity proportional to some function of local luminance level. [The function might involve either divisive or subtractive inhibition, two cardinal adaptation mechanisms (Graham & Hood, 1992).] Subsequently, the effective contrast of a test pattern is affected by the spatial distribution (pattern) of aftereffects of adaptation. With this model, effective contrast for a test of the same luminance polarity as the mask will be sharply reduced, thus raising contrast threshold. For opposite-polarity stimuli, effective contrast would be enhanced since adaptation effectively reverses mask image contrast, with a consequent reduction in threshold reduced (a sensitization).

These potentially potent effects of patterned luminance adaptation are not, however, consistent with the present results. Contrary to the referee's model, threshold elevation is greater for opposite-polarity than for same-polarity test and mask (data of KC, cf. the ○

function in Fig. 2 with that in Fig. 3). In the referee's model, luminance adaptation produces an aftereffect (afterimage) that affects test contrast. The present pattern–polarity masking effects are in the opposite direction from the presumed influence of such a retinal adaptation process. As I will discuss, the effects are instead manifestations of neuronal ON and OFF pathway isolation and interaction.

As a technical matter, I note that masking with either incremental or decremental uniform fields shifts the *mean luminance* and thus the calculated *contrast* of superimposed test stimuli. As explained in Bowen and Wilson (1994), to provide a consistent threshold metric in Equation 3, I reckon test threshold as ΔL, the change in luminance at the extreme of the D6 test stimulus. ΔL equals the product of test contrast and the mean luminance.

The results of the two-process analysis are given in Figs 4–6. Figure 4 (observer RWB) and Fig. 5 (observer KC) give data for light bar masking of positive (a) and

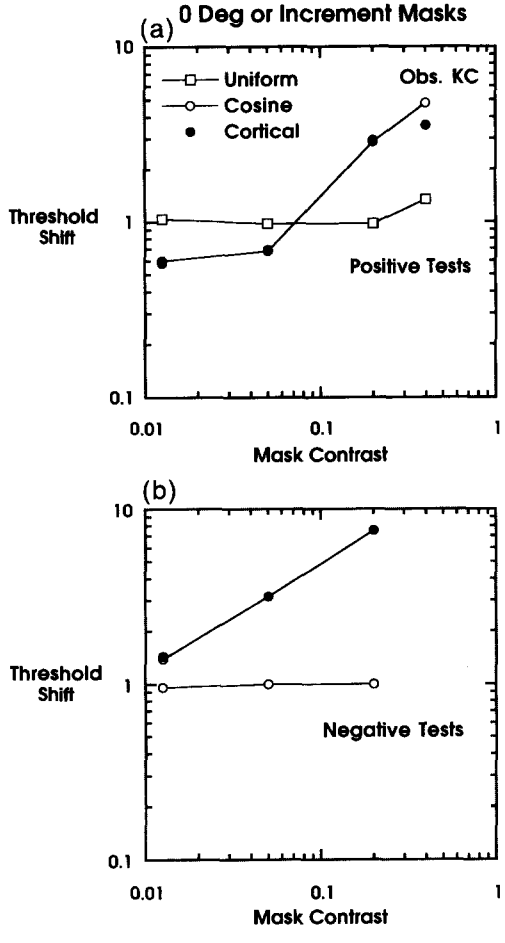

FIGURE 4. Contrast discrimination data from a two-process analysis of pattern masking. Plots show threshold shift (masked contrast threshold divided by unmasked contrast threshold) as a function of mask contrast. The open symbols represent threshold ΔC values from Fig. 2. □ Masking of D6 tests [(a) positive, (b) negative] by incremental uniform fields at luminance levels corresponding to the peak luminance in cosine masks of the indicated contrasts. ● Calculated threshold shift occurring at pattern-selective (cortical) levels. This is calculated as cosine threshold shift (total threshold shift) divided by uniform field threshold shift. Data for observer KC. See text for further details of the analysis.

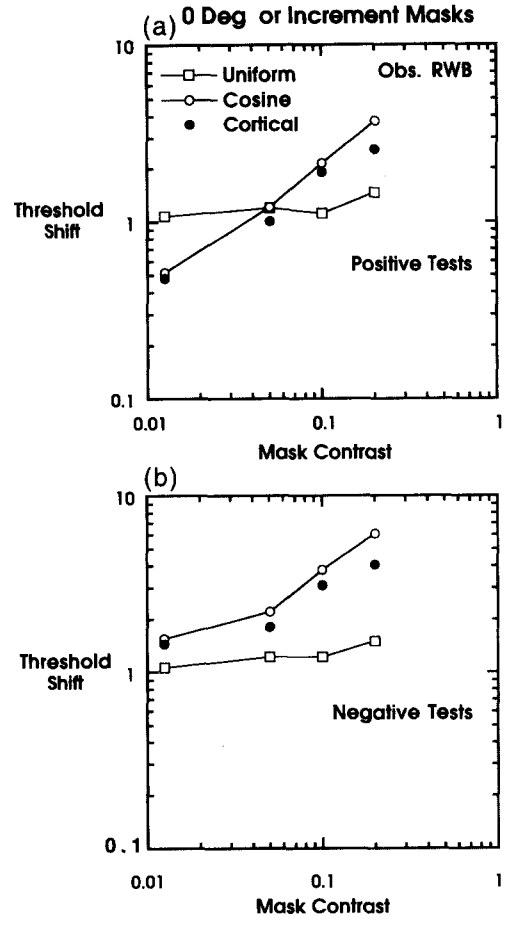

FIGURE 5. Data and analysis as in Fig. 4. Data for observer RWB.

negative (b) D6 tests. Figure 6 gives data of observer KC for dark bar masking. In the figures, threshold shift (calculated using ΔL) is given as a function of mask contrast for cosine masks (○), uniform field masks (□) and as a cortical (late process) effect calculated from Equation 3 (●).

In Figs 4 and 5, the data for uniform field masks show that there is little threshold shift with mask luminance level. Thus the putative early masking process is responsible for very little of the overall rise in ΔC with C. For positive ΔCs (a), there is no facilitation (dipper) effect for low luminance uniform fields (increments of 0.0125 effective contrast). Comparing (a) and (b) in the two figures, it is also evident that incremental uniform fields raise threshold for positive and negative test stimuli to roughly the same degree, so there is no polarity interaction like that observed for cosine masking (Figs 2 and 3).

The cosine data in these figures are derived directly from the ΔC values given in Fig. 2 and 3. Thus data for negative tests lie above those for positive tests. The dipper effect at a mask contrast of 0.0125 is evident as a threshold shift below 1 for a positive test. This does not occur for a negative one. The putative cortical data for positive test stimuli also show a facilitation effect since the uniform field data do not. Further, most of the rise in threshold occurs as a result of the cortical masking process.

The data in Fig. 6 for dark bar masking follow a similar pattern, with effects reversed for positive vs negative tests.

Decremental uniform fields at various levels generally produce threshold shifts below 1, an increase in sensitivity due to early dark adaptation (Baker, 1963; Bowen & Wilson, 1994). As a consequence, the data for the calculated cortical effect generally lie above the data for cosine masking. The data suggest that dark bar masking (OFF pathway activation) is complementary to light bar masking (ON pathway activation). Since facilitation occurs in both cases for same-polarity test stimuli, and since the facilitation is linked to cortical processes (filled symbols), I infer that the ON and OFF pathways have similar underlying contrast–response functions at a pattern-selective level in the system. The early luminance-adaptation process is not responsible for the dipper effect and generates a small fraction of the change in ΔC with C.

EXPERIMENT 2

Kulikowski (1976) conducted a contrast discrimination experiment in which he manipulated the luminance polarity of the threshold added contrast, as I have done in Expt 1. In his experiment, both the added contrast and the base contrast were identical cosine patterns (2 × 4 deg, 5 c/deg), so that decremental and incremental added contrast served to modulate the cosine amplitude in a global manner (vs the localized contrast changes in my experiment). In addition, added contrasts were modulated at 0.5 Hz on a continuously present base contrast (vs the Crawford paradigm we employed). Despite stimulus and methodological differences, Kulikowski also reported a dipper effect when cosine contrast was incremented and a monotonic rise in threshold when cosine contrast was decremented, as in the data of Figs 2 and 3. But Kulikowski's study found no difference between incremental and decremental cosine ΔC thresholds at high C as was found here using localized, narrow-band D6 test patterns.

In order to reconcile the two studies, I replicated Kulikowski's work using a Crawford paradigm for contrast discrimination. The base contrast (mask) was 5.1 deg square, 3 c/deg, cosine pattern, as in Expt 1. The duration was 500 msec. The added contrast (test) was a spatially- overlapping cosine that could be presented in 0 deg spatial phase (incremental added contrast) or 180 deg spatial phase (decremental contrast) with the base pattern. The cosine test was again 30 msec in duration, presented at an SOA = 33 msec. The combination of brief presentation and slight onset delay of the test served to create a temporally distinct ΔC.

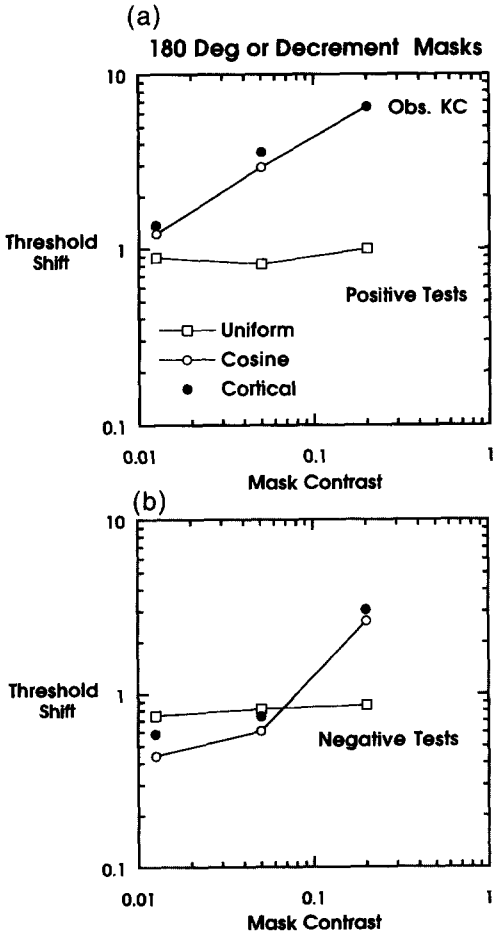

FIGURE 6. Analysis as in Fig. 4. Cosine masking data are derived from Fig. 3 and the analysis is with respect to dark-bar masking and masking by decremental uniform fields. Data for observer KC.

Results

Results for observers KC and LH are shown in Fig. 7. Observer KC replicates Kulikowski closely: a dipper function for 0 deg phase added cosine, a monotonic function for 180 deg phase added cosine when C is small, and no systematic difference between the two functions when C is large. For observer LH, the results are less systematic but contrast polarity differences are in the right direction at low C values. Kulikowski's result is replicated in spite of methodological differences.

The absence of any contrast polarity effect at higher values of base contrast is interesting. The lack of an interaction might be attributed to the 33 msec onset delay of ΔC, although ON–OFF interaction was evident at that SOA in Bowen and Wilson (1994). Alternatively, the spatially narrow-band D6 patterns used as ΔC in Expt 1 may more effectively isolate a single class of spatial-frequency selective ON and OFF pathways and index their interaction at higher C values. When ΔC is an extended cosine, a number of pattern-selective mechanisms may contribute to detection and multiple interactions might diminish observed polarity effects.

DISCUSSION

The present results indicate that contrast threshold is more evelated for opposite-polarity ΔC and C than for same-polarity stimuli, as first shown by Bowen and Wilson (1994). This interaction is shown to occur over a wide range of mask contrast levels (Figs 2 and 3). With same-polarity contrast discrimination, the relation of ΔC to C follows a dipper function, but with opposite-polarity stimuli, it is a monotonic function. Masking by incremental or decremental uniform fields (reflecting early luminance adaptation) produces no differential

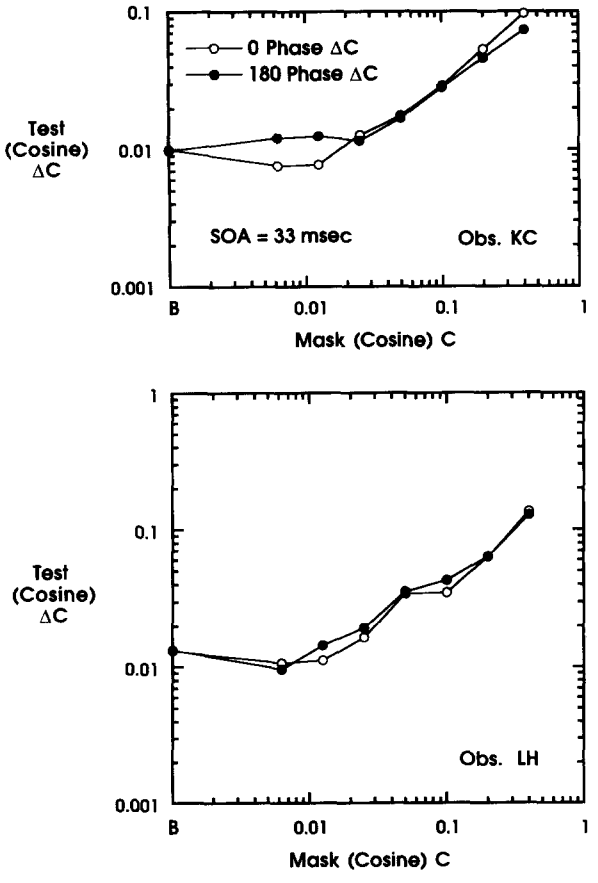

FIGURE 7. Contrast discrimination data from Expt 2. Threshold ΔC for a 30 msec, 5.1 deg square cosine test as a function of C in a 500 msec, 5.1 deg square cosine mask. The SOA was 33 msec. The test was added to the mask at 0 deg spatial phase (light bar on light bar) or in 180 deg spatial phase (dark bar on light bar). The data replicate Kulikowski (1976) as discussed in the text.

threshold elevation, and threshold facilitation is not evident with uniform field masking. The dipper effect is demonstrated here for contrast decrements as well as increments. I infer that the contrast discrimination is mediated at a pattern-selective level of processing (cortical pathways) through parallel ON and OFF pathways. I intend to discuss how these psychophysical results imply isolation and interaction of ON and OFF pathways in contrast discrimination.

As Nachmias proposed nearly 25 yr ago (Nachmias & Kocher, 1970), a given pathway makes use of an accelerated contrast–response function to heighten sensitivity at near-threshold contrast levels (the dipper effect). Clearly, the data of Figs 2 and 3 could be modeled with an accelerated nonlinearity in the contrast–response. This is so (Nachmias & Sansbury, 1974) because as the base contrast stimulus forces the point of discrimination up the response function to generate a threshold response (ΔR), a progressively smaller ΔC is required for increment detection. I am suggesting that the OFF pathway incorporates the same nonlinearity as the ON pathway, since negative contrast discrimination also follows a dipper relation (Fig. 3).

The contrast–response of cortical simple cells incorporates a low-contrast nonlinearity that could generate facilitation of contrast discrimination. The response is described by a Naka–Rushton relation (Naka & Rushton, 1966):

$$F(c) = R_{max}c^n/(c^n + \sigma^n) \quad (4)$$

where $F(c)$ is the cell's response, R_{max} is the maximum response possible from the cell, c is contrast, σ is the contrast yielding half the maximum response, and n is a constant. When $n = 1$, the response is nearly linear with contrast up to σ; this is the case for neurons in retina and lateral geniculate nucleus (Derrington & Lennie, 1984). But to fit the response of cortical neurons requires values of $n = 2$ or more (Albrecht & Hamilton, 1982; Sclar, Lennie & DePriest, 1989). In that case the contrast–response is accelerated over the lower range of C, and thus can predict the low-contrast facilitation of contrast discrimination. I interpret a dipper relation for same-polarity positive or negative contrast discrimination as isolation of the cortical ON or OFF pathway.

I want to relate the present results to a dual-pathway ON–OFF model. But first we must consider the predictions of a single-pathway model of contrast processing. I will do so in two ways, with reference to a single underlying contrast–response in the pathway, and with reference to a single type of cortical receptive field determining the spatial filtering of the pathway.

Many models of pattern processing are essentially single-pathway in that they recognize no OFF pathway (e.g. Legge & Foley, 1980). A single-pathway model of contrast discrimination proposes that both negative and positive contrast changes are mediated by a single pathway utilizing a single "static" nonlinear contrast–response. Functions for same and opposite-polarity contrast discrimination must be accounted for by such a model. If the nonlinearity is accelerated at low contrast levels, we would have the situation depicted in at the top of Fig. 8. At threshold, to produce a response to contrast increment ($+\Delta R$) requires less change in contrast as base contrast increases from C_1 to C^2. Thus the dipper, facilitation of contrast threshold, is accounted for. But threshold facilitation also is predicted to occur for responses to contrast decrements ($-\Delta R$) as is evident from the figure. When C is a contrast increment and ΔC is a decrement, a dipper relation should be obtained. But this prediction is incorrect (Fig. 2, ●).

To predict the outcomes for *decremental* masks, we must invert the nonlinear contrast–response, as at the bottom of Fig. 8. Now this depicts responses to decremental masks where C_2 is a small mask decrement down from a certain level and C_1 is the larger mask decrement. In other words, increasing decrement is equivalent to decreasing increment. Thus decrements in contrast are following a decelerated or compressive response function. The size of the contrast step required for detection now increases with contrast, since the response level is riding back down the nonlinearity from high positive to high negative (low positive) contrast. The single-pathway model therefore predicts a monotonic relation for positive test-negative mask, and this is a correct prediction. But it also predicts a monotonic relation for discrimination of a negative ΔC upon a

negative C. The model fails thus to correctly predict a dipper relation for negative contrast discrimination (Fig. 3, ●).

A single-pathway model can also take the form of specifying a single receptive field, say an ON-center field. The stimulus that most strongly activates the pathway presents light at the center of the field and dark in the inhibitory flanks. This would occur with a cosine grating of appropriate spatial frequency at 0 deg spatial phase or with a positive D6 centered on the receptive field. Conversely, the pathway is most inhibited by a cosine pattern at 180 deg spatial phase or a centered negative D6. The receptive field model thus predicts the greater degree of masking for opposite-polarity test and mask because of opposing effects of stimuli that are positive or negative to the ON-center field. However, the model also predicts little or no masking if the mask is at 90 deg spatial phase relative to the receptive field. A 90 deg phase stimulus is at a "null point" for the pathway, producing no net excitation or inhibition (Pollen & Ronner, 1981).

However, Lawton and Tyler (1994) recently compared 0 and 90 deg phase masking and found essentially equivalent masking by the two phase conditions. This result clearly requires more than a single pathway with a simple-cell receptive field profile. Lawton and Tyler suggest that masking either involves pathways with non-linear summation (e.g. complex cells) or that the masking effect occurs after phase-insensitive pooling of simple cell responses. The dual-pathway model a masker of 90 deg spatial phase could produce masking effects from pathways of both same and opposite polarity as the test stimulus. The result would be at least as much masking as is obtained with same-polarity (0 deg spatial phase) stimuli. Lawton and Tyler did not consider the possible role of ON–OFF interaction, which I consider the most parsimonious explanation of contrast polarity masking effects.

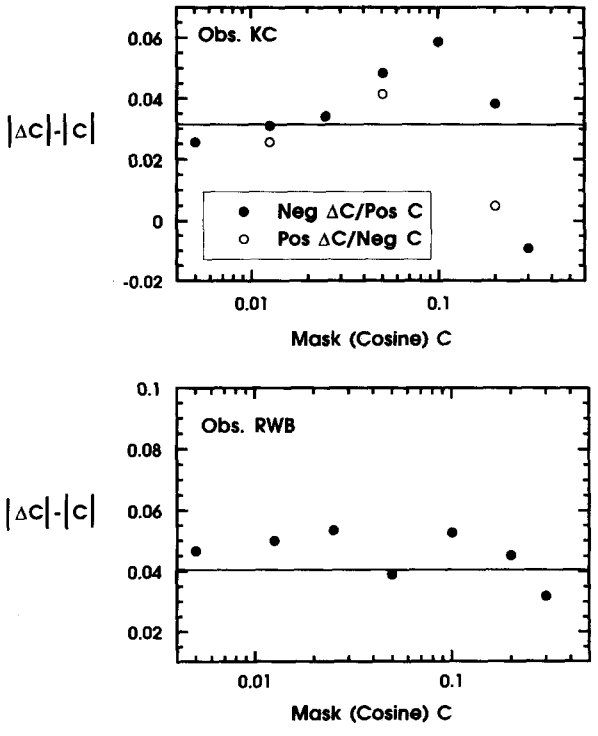

FIGURE 9. Functions for two observers showing the quantity $|\Delta C| - |C|$ as a function of C for opposite-polarity ΔC and C. The horizontal lines represent the unmasked contrast thresholds. ● Data for negative tests taken from Fig. 2; ○ data for positive tests taken from Fig. 3.

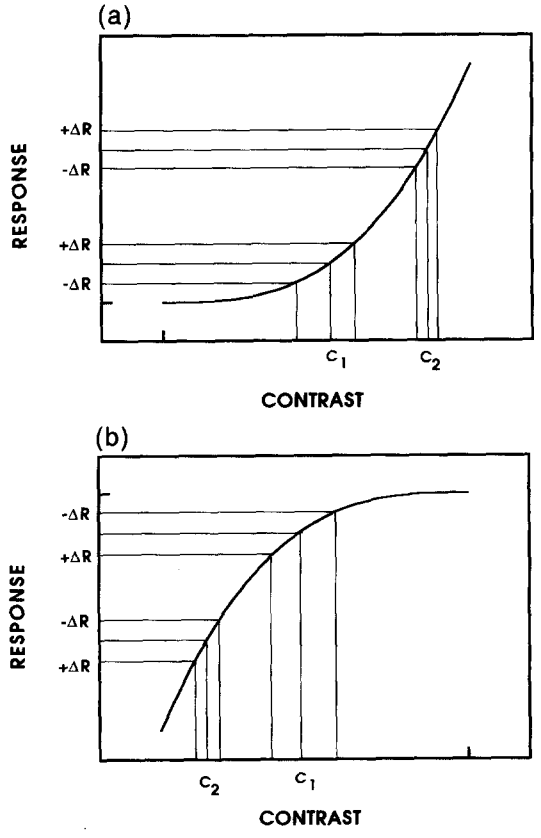

FIGURE 8. Graphic analysis of contrast discrimination by a hypothetical single neural pathway. The contrast–response of the pathway at low contrasts is a nonlinear accelerated function. (a) The detection situation for base contrast increments to levels C^1 (low) and C_2 (high). (b) The detection situation for base contrast decrements to levels C_2 (now low) and C_1 (now high). See text for complete analysis.

Since I can rule out various versions of a single-pathway hypothesis, I turn to the idea that contrast processing occurs in parallel ON and OFF pathways separately signaling increments and decrements in contrast. Many recent models of luminance adaptation mechanisms (e.g. Hayhoe, Benimoff & Hood, 1987; Graham & Hood, 1992) and of pattern-selective mechanisms (Foley, 1994) propose that prior to a static nonlinear response function (e.g. a Naka–Rushton function of luminance or of contrast), there is a stage of gain or response control that alters mechanism sensitivity to prevent response saturation. The models suggest that control signals might be of two forms: *subtractive* (as in adding a negative quantity to a positive response) or *divisive* (as in multiplying the gain by a factor of < 1.0). The present results indicate that such response control signals can arise from the pathway of opposite polarity.

My data further suggest that some between-pathway response control seems to be operating over the entire contrast range for opposite-polarity contrast discrimination (the monotonic function of Figs 2 and 3). Consider

first a simple subtractive control process. Fig. 9 shows a plot intended to show how closely opposite-polarity contrast discrimination is described by a subtractive model in which the contrast of negative test must exceed the contrast of the positive mask in order to be detected as a decrement. Using the data of Figs 2 and 3 for opposite-polarity stimuli, Fig. 9 plots the quantity $|\Delta C| - |C|$ as a function of C. The horizontal line represents the unmasked contrast threshold ($C = 0$, the "Blank" of Figs 2 and 3). The quantity $|\Delta C| - |C|$ is positive whenever the test contrast (of one polarity) exceeds the mask contrast (of the opposite polarity). This quantity allows us to neglect the actual polarity, positive or negative, of ΔC and C.

First, with the exception of the highest base contrast for observer KC, values of $|\Delta C| - |C|$ are all positive at the contrast threshold. This means that a negative test on a positive mask is detected as a contrast *decrement* below mean luminance (or a positive test on a negative mask is detected as a contrast *increment* above mean luminance, open circles, observer KC). This implies isolation of pathway response: a decremental test must be detected *as a decrement*, a positive test *as an increment*. The test contrast must be increased until the response in the detection pathway cancels the subtractive inhibition produced by the other pathway. At that point, the test is detected in the polarity-appropriate pathway, ON for positive ΔC, OFF for negative.

Second, a subtractive model holds that the residual detected decrement or increment should be of constant size and proportional to the unmasked threshold (data points on or parallel to the horizontal lines in Fig. 9). For both observers at low contrasts up to 0.025, the subtractive model is approximately true.

It is interesting that the dipper and the monotonic effects were evident with cosine test and mask in Expt 2. This also implies a low-contrast subtractive interaction between ON and OFF pathways. Kulikowski understood that the elevation of threshold for the 180 deg spatial phase condition implied that the test cosine was detected as a decremental contrast reversal: "... conversely the decrements require more change in contrast to reach the same threshold, since the background contrast has to be exceeded as well" (Kulikowski, 1976, p. 1425). He did not interpret this as interaction and isolation of the OFF pathway.

At contrast levels higher than 0.025, the data points first rise above the horizontal line, then fall, and the subtractive model does not fit. In Fig. 2, at high contrasts, the contrast discrimination functions are well-described by power functions with slopes < 1.0 (Legge, 1981). For both observers, slopes for positive and negative D6 tests are nearly equal, differing by 0.024 (RWB) and 0.069 (KC). Since these are double-log coordinates, equal slopes indicate that the contrast threshold functions differ by a constant factor, which implies that the opposite-pathway control signal is divisive at higher contrasts. Foley's (1994) recent model of same-polarity contrast discrimination also postulates divisive inhibition as a form of contrast normalization.

It has been suggested that the visual system evolved parallel ON and OFF pathways to efficiently code increments and decrements in light level or contrast (Schiller, 1992). Coding this information as increases or decreases in the response of a single pathway is limited by the fact ganglion cells have low spontaneous firing rates and therefore inefficiently code decrements as a decrease in spike rate. Separate retinal ON and OFF pathways solve the coding problem and double the dynamic range by responding selectively to input increment or decrement.

I propose that ON and OFF pathways developed because the system cannot rely on the information presented by transient *decreases* in pathway response. This is so because between a decrease in response due to a decease in contrast is confounded with a decrease in response brought about by contrast gain control. Bowen and Wilson (1994) showed that temporal changes in contrast gain are rapid, with a steep threshold decline in the first 50 msec of mask exposure. Since control of gain is so advantageous in keeping the system responsive over a broad dynamic range and preventing response saturation, the system copes by registering a true transient decrease in positive or negative contrast with an increase in the response of the OFF or ON pathway. This hypothesis would also explain why decrements are not detected as a decrease in the activity in the ON pathway (Figs 2 and 9), even though the pathway should be capable of registering the large ΔC required at high values of C. In fact, if the underlying ON-pathway contrast–response function is compressive at high contrasts (Legge & Foley, 1980), the threshold for decrement detection in that pathway should be smaller than that for increment detection (Bowen, Pokorny & Smith, 1989), but the opposite is obtained in the data.

Heeger (1992) has suggested that the control signal for normalization comes from pooling of responses of cortical units at all preferred orientations and at nearby spatial frequencies. Bowen and Wilson (1994) proposed that ON–OFF interaction might also be a fundamental form of contrast normalization. Inhibition of the response of the opposite-polarity pathways guarantees that only one mechanism is active in representing pattern contrast at a particular retinal locus. The polarity-appropriate channel thus remains as sensitive as possible both near and above threshold.

A final issue here is the validity of extant hypotheses to account for the low-contrast facilitation of discrimination. Various investigators have suggested, as I do, that the dipper effect is caused by an accelerated nonlinearity in the underlying contrast–response function at low contrast values. An alternative model, the "channel uncertainty" hypothesis (Nachmias & Kocher, 1970; Lasley & Cohn, 1981; Pelli, 1985) states that increasing C at low levels leads to increasing certainty about the location and time of occurrence of the added contrast signal. Increasing certainty reduces the number of unstimulated visual "channels" that the observer must sample, thus reducing the overall noise obscuring the signal (Lasley & Cohn, 1981). This leads to a progressive dip in ΔC.

In the present experiments, extrinsic uncertainty is minimized to the extent that the spatial frequency of ΔC and C were identical, the SOA and the duration of stimuli was fixed, and the observer's fixation was restricted to a small foveal region. Further, the reduction in uncertainty affected by raising the contrast of the mask should impact equally on decremental and incremental added contrast signals. The uncertainty hypothesis will not account for a monotonic contrast discrimination function for opposite-polarity test and mask. The monotonic effect implies that uncertainty is actually increasing over the same range of mask contrasts that supposedly reduces uncertainty for same-polarity stimuli. The uncertainty hypothesis could possibly be modified with additional (arbitrary) assumptions to account for the monotonic effect. However, it seems that the contrast discrimination functions reported here are more parsimoniously understood as reflecting underlying contrast–response functions and pathway interactions.

REFERENCES

Albrecht, D. G. & Geisler, W. S. (1991). Motion selectivity and contrast–response function of simple cells in the visual cortex. *Visual Neuroscience*, *7*, 531–546.

Albrecht, D. G. & Hamilton, D. B. (1982). Striate cortex of money and cat: Contrast response function. *Journal of Neurophysiology*, *48*, 217–237.

Baker, H. D. (1963). Initial stages of light and dark adaptation. *Journal of the Optical Society of America*, *53*, 98–103.

Bowen, R. W. & Wilson, H. R. (1994). A two-process analysis of pattern masking. *Vision Research*, *34*, 645–657.

Bowen, R. W., Pokorny, J. & Smith, V. C. (1989). Sawtooth contrast sensitivity: Decrements have the edge. *Vision Research*, *29*, 1501–1509.

Bowen, R. W., Pokorny, J., Smith, V. C. & Fowler, M. (1992). Sawtooth contrast sensitivity: Effects of mean illuminance and low temporal frequencies. *Vision Research*, *32*, 1239–1248.

Bradley, A. & Ohzawa, I. (1986). A comparison of contrast detection and discrimination. *Vision Research*, *26*, 991–997.

Campbell, F. W. & Kulikowski, J. J. (1966). Orientational selectivity of the human visual system. *Journal of Physiology, London*, *187*, 437–445.

Crawford, B. H. (1947). Visual adaptation in relation to brief conditioning stimuli. *Proceedings of the Royal Society of London B*, *134*, 283–300.

Derrington, A. M. & Lennie, P. (1984). Spatial and temporal contrast sensitivities of neurones in lateral geniculate nucleus of macaque. *Journal of Physiology, London*, *357*, 219–240.

DeValois, R. L., Jacobs, G. H. & Jones, A. E. (1962). Effects of increments and decrements of light on neural discharge rate. *Science*, *136*, 986–988.

Dolan, R. P. & Schiller, P. H. (1994). Effects of ON channel blockade with 2-amino-4-phosphonobutyrate (APB) on brightness and contrast perception in monkeys. *Visual Neuroscience*, *11*, 23–32.

Fiorentini, A., Baumgartner, G., Magnussen, S., Schiller, P. & Thomas, J. (1990). The perception of brightness and darkness: Relations to neuronal receptive fields. In Spillmann, L. & Werner, J. (Eds), *Visual perception: The neurophysiological foundations*. New York: Academic Press.

Foley, J. M. (1994). Human luminance pattern-vision mechanisms: Masking experiments require a new model. *Journal of the Optical Society of America, A*, *11*, 1710–1719.

Georgeson, M. A. & Georgeson, J. M. (1987). Facilitation and masking of briefly presented gratings: Time–course and contrast dependence. *Vision Research*, *27*, 369–379.

Graham, N. & Hood, D. C. (1992). Modeling the dynamics of light adaptation: The merging of two traditions. *Vision Research*, *32*, 1373–1393.

Hayhoe, M. M., Benimoff, N. I. & Hood, D. C. (1987). The time course of multiplicative and subtractive adaptation processes. *Vision Research*, *27*, 1981–1996.

Heeger, D. J. (1992). Normalization of cell responses in cat striate cortex. *Visual Neuroscience*, *9*, 181–197.

Hubel, D. H. & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology, London*, *195*, 215–243.

Jung, R. (1973). Visual perception and neurophysiology. In Autrum, H., Jung, R., Loewenstein, D., MacKay, D. & Teuber, H. (Eds), *Handbook of sensory physiology, Vol. VII/3A: Central processing of visual information*. Berlin: Springer.

Kuffler, S. W. (1953). Discharge patterns and functional organization of mammalian retina. *Journal of Neurophysiology*, *16*, 37–68.

Kulikowski, J. J. (1976). Effective contrast constancy and linearity of contrast sensation. *Vision Research*, *16*, 1419–1431.

Lasley, D. J. & Cohn, T. E. (1981). Why luminance discrimination may be better than detection. *Vision Research*, *21*, 273–278.

Lawton, T. B. & Tyler, C. W. (1994). On the role of X and simple cells in human contrast processing. *Vision Research*, *34*, 659–667.

Legge, G. H. (1981). A power law for contrast discrimination. *Vision Research*, *21*, 457–467.

Legge, G. E. & Foley, J. M. (1980). Contrast masking in human vision. *Journal of the Optical Society of America*, *70*, 1458–1471.

MacLeod, D. I. A., Williams, D. R. & Makour, W. (1992). A visual nonlinearity fed by single cones. *Vision Research*, *32*, 347–363.

Movshon, J. A., Thompson, I. D. & Tolhurst, D. J. (1978). Spatial and temporal contrast sensitivity of neurones in areas 17 and 18 of the cat's visual cortex. *Journal of Physiology, London*, *283*, 101–120.

Nachmias, J. & Kocher, E. (1970). Visual detection and discrimination of luminance increments. *Journal of the Optical Society of America*, *60*, 382–389.

Nachmias, J. & Sansbury, R. V. (1974). Grating contrast: Discrimination may be better than detection. *Vision Research*, *14*, 1039–1042.

Naka, K. I. & Rushton, W. H. (1966). S-potentials from colour units in the retina of fish (Cyprinidae). *Journal of Physiology, London*, *185*, 587–599.

Pelli, D. G. (1985). Uncertainty explains many aspects of visual contrast detection and discrimination. *Journal of the Optical Society of America A*, *2*, 1508–1532.

Phillips, G. C. & Wilson, H. R. (1984). Orientation bandwidths of spatial mechanisms measured by masking. *Journal of the Optical Society of America A*, *1*, 226–232.

Pollen, D. A. & Ronner, S. F. (1981). Phase relationships between adjacent simple and complex cells in the visual cortex of the cat. *Science*, *212*, 1409–1411.

Quick, R. F. (1974). A vector-magnitude model of contrast detection. *Kybernetik*, *16*, 1299–1302.

Schiller, P. (1992). The ON and OFF channels of the visual system. *Trends in Neurosciences*, *15*, 86–91.

Sclar, G., Lennie, P. & DePriest, D.D. (1989). Contrast adaptation in striate cortex of Macaque. *Vision Research*, *29*, 747–755.

Tyler, C. W., Chan, H. & Liu, L. (1992). Different spatial tunings for ON and OFF pathway stimulation. *Ophthalmic and Physiological Optics*, *12*, 233–240.

Wilson, H. R., McFarlane, D. K. & Phillips, G. C. (1983). Spatial frequency tuning of orientation selective units estimated by oblique masking. *Vision Research*, *23*, 873–882.

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